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The motion-induced position shift depends on the visual awareness of motion

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Abstract

Visual motion signals distort the perceived positions of briefly presented stimuli; a briefly-flashed, stationary stimulus appears spatially displaced in the direction of a nearby motion. The present study examined the role of the visual awareness of motion in the motion-induced position shift by using exclusive dominance and suppression of binocular rivalry. Observers dichoptically viewed a flickering radial checkerboard and two sinusoidal gratings that drifted vertically in opposite directions. When observers viewed exclusively either the checkerboard or motion stimulus, two horizontal lines were flashed, one for each side of the rivalry stimulus. During the exclusive dominance of the grating motion, the lines appeared to shift in the directions of the nearby motions. The position shift was identical to that during non-rivalry, monocular viewing of the motion stimulus. However, when the grating motions were completely suppressed, no position shift was observed. These results demonstrate that the motion-induced position shift depends on the visual awareness of motion.

Keywords: Binocular rivalry; Motion; Position; Awareness

1. Introduction

Perceiving the position of a visual object is far from an easy task, particularly when a visual scene is dynamic. This is because motion and position signals interact in the visual system (De Valois & De Valois, 1991; Whitney, 2002). In particular, the perceived geometrical relationship among briefly presented visual stimuli is influenced by motion signals in the visual field; a briefly-flashed stationary stimulus (e.g., a line) appears to be spatially displaced in the direction of a nearby motion signal (Whitney & Cavanagh, 2000). Several studies have investigated conditions under which the motion-induced position shift of distant stationary objects occurs (Durant & Johnston, 2004; Shim & Cavanagh, 2004; Watanabe, Nijhawan, & Shimojo, 2002; Watanabe, Sato, & Shimojo, 2003). These studies have clarified that the illusory shift in position can be produced by real motion, illusory motion, and inferred motion. These observations suggest that the illusory position shift is a relatively ''high-level'' perceptual effect, a possibility that I set out to test in the present experiment. In particular, the present study examined whether the position shift occurs when the normally effective inducing motion is erased from conscious awareness by binocular rivalry suppression.

Binocular rivalry occurs when the two eyes receive significantly different visual inputs (Breese, 1909). Even though the physical characteristics of these dissimilar monocular inputs remain constant, the observer viewing them experiences phenomenal competition between the two incompatible views. Interleaved with the ''mixed''

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or "piecemeal" perceptual experience, one entire image will be suppressed from visual awareness for several seconds at a time, and its competitor will completely dominate the visual perception. By comparing the behaviors of the visual system in these periods of complete dominance and complete suppression, it is possible to examine the role of visual awareness of a particular specific stimulus aspect for a certain task, while maintaining physical inputs to the visual system (Blake, 1997; Blake & Logothetis, 2002). A number of studies have exploited this characteristic of binocular rivalry and pinpointed aspects of visual processing relative to the site of binocular suppression (e.g., Blake & Fox, 1974; Blake, Yu, Lokey, & Norman, 1995; Lehmkuhle & Fox, 1975; van der Zwan & Wenderoth, 1994; Wade & Wenderoth, 1978; Watanabe, Paik, & Blake, 2004). Certain visual functions, aftereffects, and other measurable phenomena survive binocular rivalry suppression (i.e., rendering retinal inputs invisible); these include the orientation-specific adaptation (Blake & Fox, 1974), linear motion aftereffect (Lehmkuhle & Fox, 1975; O'Shea & Crassini, 1981), contrast gain modulation (Watanabe et al., 2004), two-frame apparent motion (Wiesenfelder & Blake, 1991), and global motion perception (Andrews & Blakemore, 1999). However, other (mostly higher-order) visual functions appear to be dependent on the visual awareness of the stimulus (e.g., Chen, Matthews, & Qian, 2001; Moradi, Koch, & Shimojo, 2005; van der Zwan, Wenderoth, & Alais, 1993; Wiesenfelder & Blake, 1990). In the current study, we examined how the motion-induced position shift operates with and without visual awareness of the motion by utilizing exclusive dominance and suppression periods of binocular rivalry.

2. Methods

2.1. Observers

Seven observers, including the author, participated in the experiment. All the observers, other than the author, were naive about the objective of the experiment. All had normal or corrected-to-normal vision.

2.2. Stimuli

A schematic of the dichoptic visual display is shown in Fig. 1. Visual stimuli were displayed on a gamma-corrected CRT monitor ($19.2° \times 25.6°$, 60 Hz refresh rate) in a dark room. In each trial, one eye was made to view a pair of sinusoidal gratings (3.3 cycle/deg; 3.0° in size) that drifted vertically in opposite directions (3.0 deg/s), and the other was made to view a flickering radial-checkerboard (20 Hz; 3.0° in size). These dichoptic stimuli were presented against a mid-level gray (29 cd/m^2) background. The maximum Michelson contrast of the checkerboard was 40%, whereas that of the grating was 20%. These values were determined before the experiment to ensure that the observers could not view the suppressed stimulus but could still experience a reasonable number of alternations in the perceptual state during an extended viewing period. In order to support the steady fixation and binocular overlap between the grating and checkerboard, both stimuli were presented with white fixation crosses (58 cd/m^2, 0.25°) and placeholders. The directions of the motion gratings were reversed with intervals chosen randomly from 2 s to 3 s. The grating was presented to a predetermined eye in each session, which was counterbalanced among sessions.

2.3. Procedure

Observers viewed the visual stimuli dichoptically using a haploscope. In each trial, when the grating motion stimulus achieved a designated phenomenal state (dominance or suppression condition that was pre-specified for each session), observers pressed a key to initiate the transient presentation (16.7 ms) of two horizontal lines (58 cd/m^2, 0.025° thick, 0.25° long). When the observer pressed a key, the directions of the grating motions were reversed. The lines were presented 0–200 ms after the reversal of the grating motions (c.f., Whitney & Cavanagh, 2000), one at each side of the rivalry stimulus. These lines were vertically misaligned from the eye level (i.e., from the fixation cross) in opposite directions. The vertical offset of the lines was randomly varied to achieve nine offset conditions ($-32, -16, -8, -4, 0, +4, +8, +16, +32$ arcmin in the direction of the post-flash motion). The two lines were presented with either the motion stimulus (same-eye condition) or the checkerboard stimulus (opposite-eye condition) so that the eye that received the line presentation was counterbalanced. The entire stimulus disappeared 400 ms after the line presentation. The observers were instructed to avoid initiating the line presentation during the transitory phases between dominance and suppression (i.e., during the "piecemeal" rivalry). In addition, if any perceptual transition occurred at or after the instance of line presentation, the observers were asked to press a cancel button to discard the trial; the same trial reappeared later in the session. After successful initiation of the line presentation, the observers indicated whether the left line was higher than the right line or conversely (2AFC) by pressing appropriate keys. No error feedback was given. In a session, for each combination of 9 offset conditions and 2 eye conditions, 5 trials were repeated (90 trials). Each observer attended 8 sessions for each of the dominant and suppression conditions, resulting in a total of 16 sessions for the main experiment.

In the control experiment (monocular condition), the contrast of the checkerboard was set to zero. Hence, the

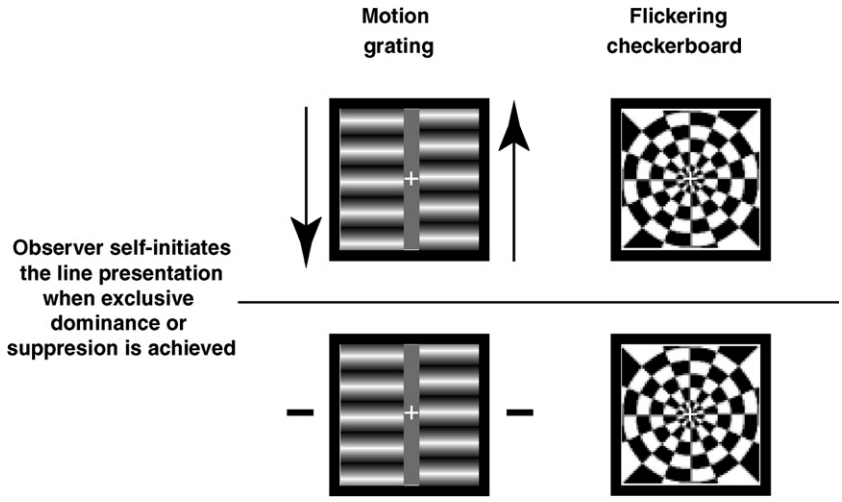

Fig. 1. Schematic presentation of visual stimulus. Observers viewed a pair of sine-wave gratings that drifted vertically in opposite directions and a flickering radial checkerboard dichoptically, leading to perceptual alternation between them. When the observers exclusively saw either the grating motion (dominant condition) or the flickering checkerboard (suppression condition), two horizontal lines were flashed with various vertical offsets, one at each side of the rivalry stimulus. In the control experiment, only the grating motion stimulus was presented monocularly.

observers only viewed the grating motion stimulus presented monocularly. The procedures were identical to those used in the main experiment, except that the observers initiated the line presentation upon hearing a 1000 Hz beep from the computer speaker. The auditory signal was delivered with a delay from the beginning of a trial. The delay was determined randomly from the observer's wait durations (i.e., time elapsed from the start of a trial to when a key press occurred), which were separately recorded in the dominant (monocular-D-duration condition) and suppression sessions (monocular-S-duration condition) of the main experiment. This was done to make the observation durations in the control experiment similar to those in the main experiment. The observers attended 8 control sessions for both the monocular-D-duration and monocular-S-duration conditions.

3. Results

On an average, 3.2% of the trials were cancelled during one session. The top panels of Fig. 2 show the percentage of trials in which the lines appeared to be displaced in the direction of the nearby motion (averaged for all observers) as a function of the physical misalignment of the lines in the directions of the motions. The averaged data were fitted with the logistic function, $y = C[1 + \exp\{-a(x - b)\}]^{-1}$. When the observers exclusively saw the grating motion (dominance condition), the flashed lines were perceived as displaced in the directions of the nearby motions. This was true irrespective of whether the lines were presented to the eye that received the grating (same-eye condition; left panel) or to the eye viewing the checkerboard (opposite-eye condition; right panel). On the other hand, when the grating motion stimulus was completely suppressed from visual awareness (suppression condition; i.e., when the observers saw exclusively the flickering checkerboard), no position shift was found. This was also true for both the same-eye and opposite-eye conditions. It should be stressed that failure to observe an illusory motion shift when the motion was suppressed was not because it was more difficult to see the lines themselves. The lines were imaged outside the region of rivalry and, therefore, always visible. Further, to reiterate, the illusory shift was vanished regardless of which eye received the two horizontal lines. The motion-induced position shift was clearly observed during the monocular view of the grating motion stimulus in both the monocular-D-duration and monocular-S-duration conditions. Again, there was no difference between the same-eye and opposite-eye conditions.

The magnitude of the position shift for each observer was estimated by deriving a psychometric function from the data of each observer (fitted with the logistic function) and calculating 50% points. The bottom panel of Fig. 2 shows the averaged estimations of the position shifts. A three-way ANOVA indicated significant main effects of the rivalry condition (rivalry vs. monocular; $\underline{F}(1,6) = 6.94$, $\underline{p} < 0.05$) and the perceptual state or observation duration (dominance vs. suppression; $\underline{F}(1,6) = 15.09$, $\underline{p} < 0.05$). It must be noted that, in the monocular conditions, "dominance" and "suppression" refer to the observation durations recorded in the main rivalry experiment, not to the perceptual state when the lines were presented. The factor of presentation eye did not show a significant main effect (same vs. opposite,

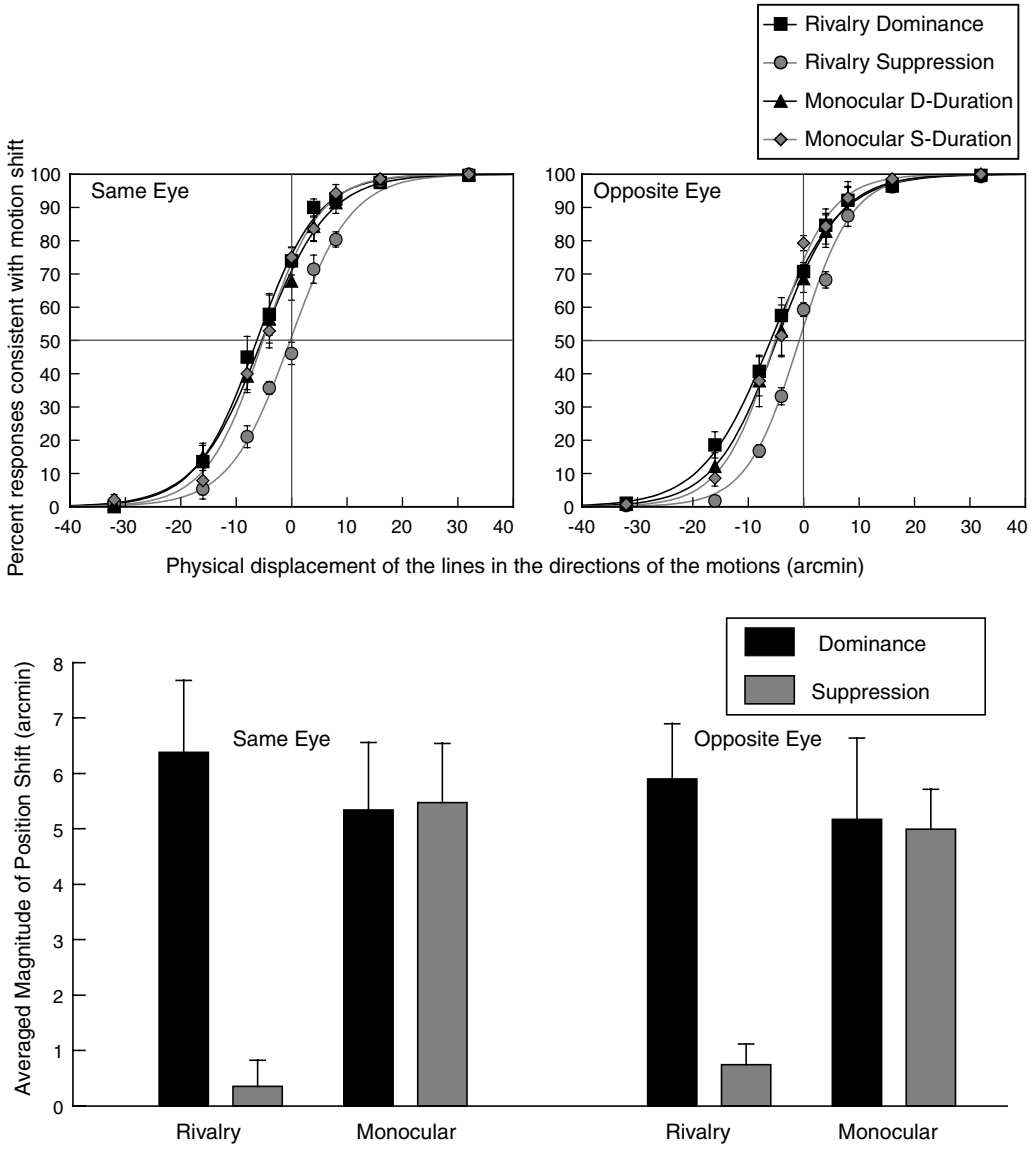

Fig. 2. (Top) Percentage responses consistent with motion shift (i.e., the "the lines are displaced in the direction of the nearby motion" responses) as a function of physical displacement of the lines in the directions of the motions, averaged across all observers (Left panel, same-eye condition; Right panel, opposite-eye condition). (Bottom) Averaged estimations of position shift. The position shifts in the suppression conditions were not statistically different from zero ($p > 0.1$), whereas the position shift was clear in the other conditions.

$F(1,6) = 0.07$, $p = 0.80$). The interaction between rivalry condition and perceptual state was significant ($F(1,36) = 14.86$, $p < 0.05$), whereas the other interactions were not. Additionally, the position shift in the suppression condition was not statistically different from zero ($t(6) < 1.97$, $p > 0.1$ for both the same-eye and opposite-eye conditions).

4. Discussion

The results of the present study demonstrate that the motion-induced position shift is vanished when the inducing motion is erased from visual awareness by binocular rivalry suppression. This finding is consistent with results obtained from other recent studies pointing to the involvement of high-level mechanisms in this illusion. For example, the perception of spatial position can be shifted even when the motion signals inducing that shift are not explicitly present in the visual field and, instead, are implied by occluded motion (Watanabe et al., 2003). Moreover, illusory position shifts can be induced by a stationary object that appears to move only because of prior adaptation (Whitney & Cavanagh, 2003). Finally, by measuring the position shift as a function of the perceived motion in a bistable quartet, it has been found that an illusory position shift occurs only when the flashes are close to the trajectory where motion is seen (Shim & Cavanagh, 2004). These findings indicate that high-level motion processes are sufficient to pro-

duce the position shift. The results from the present experiments provide complementary evidence for the same conclusion by showing that the removal of the inducing motion from conscious awareness vanishes motion-induced position shifts of stationary objects.

The conclusion from this study could be strengthened if we could specify where in visual processing binocular rivalry suppression transpires. However, this has been an issue of some controversy in recent years. Single unit recordings from alert behaving monkeys experiencing binocular rivalry reveal only a small percentage of neurons in the primary visual cortex, where responses are modulated in synchrony with the animal's report of dominance and suppression. Conversely, in higher visual areas, a larger percentage of neurons shows activity fluctuations correlated with the perceptual state (e.g., see Leopold, Murayama, & Logothetis, 2003). Brain imaging studies in humans, however, show robust modulations in neural responses (as indicated by fluctuations in blood oxygenation levels) throughout the visual pathways, including the primary visual cortex (e.g., see Tong, 2004). For the purpose of interpreting the effect of binocular suppression on the motion that induces illusory positional shifts, it is logical to believe that this suppression of motion signals transpires prior to the site at which the motion signal influence the perceived position.

It should also be noted that binocular suppression does not invariably disrupt motion processing. It is known, for example, that two-frame apparent motions can be experienced even when the first frame of the sequence is suppressed during rivalry (Wiesenfelder & Blake, 1991). In addition, motion suppressed from vision can nonetheless be combined with the dissimilar motion viewed by the dominant eye to produce global motion in a direction midway between the dominant and suppressed directions of motion (Andrews & Blakemore, 1999). The result reported in this paper, i.e., suppression of motion vanishing illusory position shifts, is consistent with earlier studies showing that suppressed motion signals disrupt only higher-order motion processing (Chen et al., 2001; van der Zwan et al., 1993; Wiesenfelder & Blake, 1990), and our study suggests that the site where motion and position processes interact may be higher than the sites of conscious awareness of visual motion.

4.1. Neural sites for motion processes that produce a position shift

The cortical activity in area MT has been shown to be closely correlated with conscious awareness of visual motion in macaque monkeys (Britten, Shadlen, Newsome, & Movshon, 1992; but see Ilg & Churan, 2004) and humans (Tootell et al., 1995). Therefore, it is likely that motion signals for the position shift originate from neural activity in area MT and related brain regions. To support this hypothesis, no difference was found between the same-eye and opposite-eye conditions in this study, replicating the results of Whitney and Cavanagh (2000). This suggests that the motion-induced position shift occurs after integration of visual information from the two eyes (i.e., after V1). Moreover, a recent study has shown that another type of motion-induced position shift, namely, the position shift induced by motion aftereffect (Snowden, 1998; Nishida & Johnston, 1999), is critically dependent on the cortical motion processing at area MT (McGraw, Walsh, & Barret, 2004). McGraw et al. (2004) demonstrated that when cortical activity in MT was disrupted by transcranial magnetic stimulation after motion adaptation, the position shift decreased significantly. In contrast, transcranial magnetic stimulation of V1 did not affect the position shift by motion adaptation. These findings point to the primary role of conscious motion perception, most likely mediated at the level of MT or higher, in the generation of motion-induced position shifts.

Motion and position signals probably interact also within MT/MST (Krekelberg, Kubischik, Hoffmann, & Bremmer, 2003; McGraw et al., 2004) rather than V1/V2. Alternatively, motion signals may be relayed to position signals via a re-entrant input stream from higher cortical areas, where the conscious perception of visual motion is established (e.g., MT/MST) to lower cortical areas, where the neural representation of spatial position resides (Pascual-Leone & Walsh, 2001).

4.2. Necessary condition for all motion-related illusory position shifts?

The results of the present study indicate that the position shift of distant stationary objects due to motion signal is disrupted when visual motion occurs outside of awareness. However, it may be premature to conclude that visual awareness of inducing motion is a *necessary* condition for all types of motion-related position shifts. For example, the position shift induced by motion adaptation was observed even when the carrier gratings of the adapting and test stimuli were orthogonal and, therefore, no motion aftereffect was experienced (McGraw, Whitaker, Skillen, & Chung, 2002). The discrepancy on the role of visual awareness in these illusory position shifts could be due to differences in stimulus configurations between the motion-adaptation-dependent position shift (McGraw et al., 2004, 2002; Nishida & Johnston, 1999; Snowden, 1998) and the motion-induced position shift (Durant & Johnston, 2004; Shim & Cavanagh, 2004; Watanabe et al., 2003; Whitney & Cavanagh, 2000). For example, in a majority of experiments using motion adaptation, the motion stimulus and a stationary object were presented at the same location (however, see Whitney & Cavanagh, 2003 as a counter-example). On the other hand, in motion-

induced position shifts, the apparent position of an object can be shifted even when the object is located away from the motion stimulus. In addition, the apparent shift of a distant stationary object requires the object to be briefly presented (Whitney & Cavanagh, 2000). One interpretation of this may be that the awareness of visual motion modulates the perceived position of a flashed object that is remotely placed from the inducing motion; but the motion awareness may not be required when an object is placed on a retinal region that is stimulated by the motion.[1] However, further psychophysical investigations are required to clarify the similarities and differences between these apparently similar phenomena.

Another possibility is that the cortical activity of MT/MST, not the awareness of visual motion, generates these motion-related position shifts. This is because, the idea that the cortical activity of MT/MST is the sole neural correlate of conscious motion perception still warrants further substantiation, and it is possible that areas MT and MST are not the final stages responsible for conscious motion perception (Ilg & Churan, 2004). Combining psychophysical and functional-neuroimaging methods would be a promising avenue for further investigations of motion-related illusory position shifts (Whitney et al., 2003)

5. Conclusion

The present study examined the relationship between the visual awareness of motion and the motion-induced position shift of briefly presented stationary objects. The results demonstrate that the motion-induced position shift is closely associated with the visual awareness of the inducing motion. In other words, the awareness of motion modulates, if not mediates, the illusory position shift. This result suggests that high-level motion processes (at the level of conscious motion perception) are involved in the positional shift (e.g., Shim & Cavanagh, 2004; Watanabe et al., 2003). However, the precise manner in which higher motion processes influence the positional signals of stationary objects and the implementation of such processes in the brain remain to be investigated.

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[1] Yet another possibility is that the perception of the flickering stimulus might disrupt the process underlying the motion-induced position shift (Durant & Johnston, 2004). In this case, it could be stated that the visual awareness of motion modulates (not mediate) the illusory shift.

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